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Variation in the abundance of sandeels *Ammodytes marinus* off southeast Scotland: an evaluation of area-closure fisheries management and stock abundance assessment methods

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In 2000, a sandeel fishery off SE Scotland, which commenced in the early 1990s, was closed in response to concerns that the fishery was having a deleterious effect on seabird breeding performance at colonies in the vicinity of the fishing grounds. Fishery-derived catch per unit effort (cpue) data are used together with three different fishery-independent survey techniques (acoustic, demersal trawl, and nocturnal grab survey) to assess variation in sandeel *Ammodytes marinus* population biomass in the area over the period 1997–2003, a period that included the last three years that the fishery was operating and the first four years of the sandeel fishing moratorium. Temporal trends in estimates of sandeel biomass derived from these different assessment methods were inconsistent and, on the basis of these alone, it was not possible to determine whether sandeel population biomass in the area had increased following the closure of the fishery. The different survey methods assess different components of the sandeel population; acoustic survey and fishery cpue quantified sandeels active in the water column, whilst demersal trawl survey quantified sandeels buried in the sediments. These data were collected at a time of year when sandeels were moving between the seabed sediments and the overlying water column. A grab survey also quantified sandeels buried in the sediment, but these data were collected at a time of year when the entire population should have been buried in the sediment. Differences between the different time-series were reconciled by taking account of the cumulative total primary production in each year prior to the surveys. On the basis of this, a model was developed that utilized acoustic and demersal trawl survey data to estimate the total sandeel population biomass. This model was validated using the nocturnal grab-survey data. The modelled data indicated that the biomass of sandeels 1+ years old increased sharply in the first year of the closure and remained higher in all four of the closure years than in any of the preceding three years, when the fishery was operating. The biomass of 0-group sandeels in three of the four closure years exceeded the biomass present in the three years of commercial fishing. Whereas the response of 1+ sandeels may have been a direct consequence of the closure, this is not likely to have been the case in respect of 0-group sandeels. The closure appears to have coincided with a period of enhanced recruit production.

Keywords: fishery closure effects, fishery-dependent assessment, fishery-independent assessment, local stock biomass assessment, sandeel behaviour modelling.

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Introduction

Fishing for small fish for industrial purposes in the North Sea commenced in the 1970s and expanded rapidly during the 1980s. Sandeels *Ammodytes marinus* are the principal species targeted by this industrial fishery. In recent decades annual landings of sandeels have topped one million tonnes on occasion, and have rarely dropped below 0.5 million tonnes (ICES, 2002, 2004). Sandeels are therefore the target of the largest single-species fishery in the North Sea (Gislason and Kirkegaard, 1998), and they also constitute important prey for many top predators. They are an important part of the diet of commercial fish species, such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*), and mackerel (*Scomber scombrus*; Daan, 1989; Daan *et al.*, 1990; Hislop *et al.*, 1991; Hislop, 1997; Greenstreet *et al.*, 1998). Several marine mammals feed intensively on sandeels during spring and early summer. Examples are grey seals (*Halichoerus grypus*; Hammond *et al.*, 1994), harbour seals (*Phoca vitulina*; Pierce *et al.*, 1991; Tollit and Thompson, 1996; Tollit *et al.*, 1997; Brown *et al.*, 2001), and harbour porpoise (*Phocoena phocoena*; Santos and Pierce, 2003). Sandeels are also the principal prey of many of the most abundant seabird species that feed in the North Sea, including common guillemots (*Uria aalge*), razorbills (*Alca torda*), Atlantic puffins (*Fratercula arctica*), northern gannets (*Morus bassanus*), and black-legged kittiwakes (*Rissa tridactyla*), particularly during the breeding season (Tasker and Furness, 1996; Wanless *et al.*, 1998; Furness and Tasker, 2000).

The North Sea sandeel stock is assessed annually and, until recently, these assessments suggested that current levels of fishing mortality were not excessive (ICES, 2002). However, there is increasing evidence that sandeels in the North Sea do not constitute a single homogenous stock, but may instead consist of several discrete stocks (Proctor *et al.*, 1998; Pedersen *et al.*, 1999). Fishing effort for the species is also patchily distributed, raising the possibility that overexploitation of sandeel stocks may have taken place at local spatial scales (Frank and Brickman, 2001). With so many marine top predators heavily reliant on sandeels, the potential for local overexploitation has increasingly given cause for concern (Ormerod, 2003). Many sandeel fishing grounds are close to major seabird colonies, so the overlap between the distributions of post-settlement sandeels, seabirds at sea, and industrial fishing activity is considerable (Jensen *et al.*, 1994; Wright and Begg, 1997). Consequently, concern has focused on the potential impact of sandeel fishing on seabird stocks (Monaghan, 1992; Furness and Tasker, 2000; Tasker *et al.*, 2000; Furness, 2002, 2003). On two occasions, in the Shetland Isles in the mid-1980s and off the Firth of Forth in SE Scotland in the mid-to-late 1990s, declines in seabird breeding success were linked to nearby sandeel fishing activity (Monaghan *et al.*, 1989; Hamer *et al.*, 1991, 1993; Furness, 1996; Wright, 1996; Harris and Wanless, 1997; Rindorf *et al.*, 2000). In both instances, a precautionary approach was adopted and the sandeel fishery in question was closed.

Such concerns, and the management response to them, highlight the necessity for monitoring changes in the abundance of sandeels in areas where marine predators might be at risk. First, there is the obvious need to monitor change in the abundance of sandeels, so that circumstances wherein the fishery may start to limit sandeel availability to predators can be recognized. Second, when fisheries are closed to alleviate such situations, the effectiveness of the management action will need to be monitored and assessed. Such information should be a prerequisite where management intent is ultimately to re-open the fishery following stock recovery. Traditionally, most information on the abundance of sandeels has originated from scientific monitoring of the fishery (Wright, 1996; Furness, 2002). Complete closures of specific sandeel fisheries will compromise the availability of such data, making monitoring of the effectiveness of a closure difficult. Furthermore, results of the analysis of fishery-derived data in the form of traditional stock assessments (ICES, 2002, 2004), or even catch per unit effort (cpue) data, are rarely available in real time. The first indications that a particular local sandeel stock might be in trouble may come after the event, by which time marine top predators in the region may already be having difficulties obtaining prey. Fishery-derived indices also suffer from the disadvantage of not being sampled randomly. This can lead to the maintenance of artificially high abundance indices if only high-density areas are sampled (Hilborn and Walters, 1992), and these are constantly replenished from more marginal habitats following some form of "ideal free" redistribution process (Fretwell and Lucas, 1970; Partridge, 1978). Such a situation has been postulated for sandeel fishing grounds off the Scottish east coast (Jensen *et al.*, 2001).

Assessing local sandeel population biomass is difficult because of the species' capacity to move freely between the seabed sediments and the overlying water column. In fact, sandeels spend most of their time buried in the sediments (Reay, 1970; Winslade, 1974a, b, c; Pinto *et al.*, 1984), emerging briefly to spawn in mid-winter (Macer, 1966; Gauld and Hutcheon, 1990; Bergstad *et al.*, 2001), and to feed in large schools during part of the day over a more prolonged period in late spring and early summer (Macer, 1966; Reay, 1970; Winslade, 1974a, b, c; Freeman *et al.*, 2004). Sampling sandeels in the sediment at night, using grabs and dredge gears for example, therefore, presents the best opportunity for assessing the entire population in one medium at one time. However, at the time of the seabird breeding season, and at latitudes that include the major seabird breeding colonies, light levels drop below 20 lux for <5 h each night. At higher light levels, emergence activity is stimulated (Winslade, 1974b). This makes it difficult to carry out sufficient nocturnal survey work in the time available. Late autumn and early spring are more appropriate for nocturnal grab or dredge surveys, when the entire population should be in the sediment and the night-time periods are longer. However, those times are well outside both the seabird breeding and main fishing seasons, making real-time management of a fishery based on such assessment methods difficult.

Assessing sandeel abundance at around the time that the fishery might operate, and when seabirds are likely to be most dependent on the species, should provide a more informative basis for a broader ecosystem approach to the management of sandeel fisheries. However, this would tend to involve surveying outside the hours of darkness at a time of year when sandeels were moving frequently between the sediment and the water column. Assessment methods relying solely on "sampling" sandeels in the water column, for example acoustic survey techniques and commercial pelagic industrial trawling cpue, are therefore open to the criticism that they fail to sample the entire population. The proportion of the sandeel population active in the water column varies considerably in response to several influences, such as variation in water temperature, light level, and zooplankton abundance, and the risk from predation (Reay, 1970; Winslade, 1974a, b, c). To add to the difficulties involved, different components of the population, for example 0-group sandeels and older sandeels, may also spend different fractions of the available time feeding in the water column and buried in the sediment (Reeves, 1994; Kvist *et al.*, 2001; Bergstad *et al.*, 2002). In terms of specific growth rates, 0-group sandeels need to gain weight to a much greater extent than older sandeels during the feeding period, so as to achieve a minimum body mass sufficient to survive the ensuing winter (Winslade, 1974c). Distinguishing interannual variation in sandeel population biomass (of both age groups) from between-survey differences in the proportion of the sandeel population active in the water column, therefore, presents difficulties in interpreting the results of such surveys when carried out in isolation.

The timing and intensity of primary production, which provides food for the main zooplankton prey of sandeels (Covill, 1959; Macer, 1966; Reay, 1970; Meyer *et al.*, 1979; Monteleone and Peterson, 1986), must strongly influence the availability of food to sandeels, and consequently affect the amount of time sandeels spend foraging in the water column (Winslade, 1974a, c). Variability in both the timing and the intensity of the spring bloom in primary production at any given location in the North Sea is driven by the degree of mixing within the water column (Le Févre, 1986; Pingree *et al.*, 1975; Simpson, 1981). As water depth and tidal current speeds at any location are deterministic (Pingree *et al.*, 1978, Simpson and Bowers, 1981), any variation in water column mixing, and hence primary production, is due to interannual differences in local meteorological forcing. Based on an earlier model (Sharples, 1999), Sharples *et al.* (2006) developed a one-dimensional, coupled biophysical model that uses daily local meteorological data to determine seasonal variation in water column mixing and primary productivity in the Marr Bank and Wee Bankie region off Scotland, areas with notable sandeel concentrations. Annual variation in the timing of the spring bloom determined by this model is correlated with kittiwake breeding success at local seabird colonies (Scott *et al.*, 2006). Since kittiwakes in this area are heavily dependent on sandeels (Wanless *et al.*, 1998; Rindorf *et al.*, 2000; Lewis *et al.*, 2001), this relationship is presumably mediated through an effect of primary productivity on sandeel behaviour. This model could therefore provide the necessary additional information required to interpret interannual variation in, for example, acoustic survey data and thus enable variation in total population biomass to be distinguished from variation in the proportion of the population active in the water column.

The sandeel fishery off SE Scotland was closed in 2000. Here we present data collected on the main fishing grounds, the Wee Bankie, Marr Bank, and Berwick's Bank, over the period 1997–2003. Our analyses include the last three years of the fishery and the first four years of the closure. Our principal aim is to determine the effectiveness of the fishery closure as a means of restoring a potentially depleted sandeel stock. First we present the basic catch, effort, and cpue data reported to the Danish Institute of Fisheries Research (DIFRES) by Danish sandeel fishers in order to determine the extent to which the closure actually modified fishing activity in the area. A limited scientific fishery was permitted to enable cpue data to be collected for scientific monitoring of the sandeel population within the closed area. We then use three fishery-independent survey methods to assess the population biomass or abundance of sandeels within the study area. We explore the relationships between these fishery-independent biomass estimates and the fishery-based cpue. In the process, we illustrate the difficulties involved in interpreting the results of the different survey techniques, caused primarily by the species' behavioural characteristic of moving between the water column and seabed sediments, and the extent to which the different survey techniques detect sandeels either in the water column or in the sediment. To overcome these problems, we use the output from a one-dimensional coupled biophysical model to reconcile the differences between temporal trends derived from the four biomass assessment techniques. We then develop a simple statistical model that utilizes the data collected from two fishery-independent survey techniques to estimate first, the proportions of the sandeel population that are either active in the water column or buried in the seabed sediments, and second, the total or absolute biomass of sandeels in the study area in each year. The model results are validated with data collected by a third fishery-independent assessment method. This model could provide biomass assessment information in real time, allowing managers the option of regulating fisheries at critical times for predator populations.

Study area and methods

The study area covered most of two ICES statistical rectangles, 41E7 and 41E8, between 56°0′N and 56°30′N, and longitudes 03°0′W and 01°0′W (Figure 1). Fishery-dependent catch and effort data are reported for both rectangles. Fishery-independent acoustic, demersal trawl, and nocturnal grab surveys were undertaken using the Scottish FRV "Clupea". All acoustic and demersal trawl survey work was carried out between 03:00 and 15:00 GMT, between late May and early July of each year from 1997 to 2003 (Table 1), and grab-survey work was undertaken between 20:00 and 04:00 GMT in October of each year from 1998 to 2003. The acoustic and demersal trawl surveys followed immediately one after the other, with one day in between to change fishing gears. The order of the surveys varied between years with the objective of minimizing variation in the timing of the acoustic survey. Because the "Clupea" could not operate throughout an entire 24-h period, it was necessary to anchor close inshore for at least 10 h each day. As a result, it was not possible to cover the two ICES rectangles completely, so an area down the eastern edge of ICES rectangle 41E8 had to be excluded. However, the area that was covered by the two surveys (east to longitude 01°30′W in the north, and to 01°10′W in the south) included the main sandbanks, the Wee Bankie, Marr Bank, and Berwick's Bank, where most sandeel fishing activity in these two ICES rectangles took place (Figure 1). The 4720-km^2 area covered by the acoustic survey included the section of water inside the Firth of Forth. This area, in the middle of a busy shipping lane, was inappropriate for demersal trawling, so was excluded from the demersal trawl area. Few sandeels were observed there during the acoustic surveys, and no commercial sandeel fishing took place there. The area covered by the demersal trawl survey was therefore bounded to the west at longitude 02°40′W and amounted to approximately 4529 km^2.

Acoustic survey

The study area was divided into 50 rectangles of 5′ latitude by 10′ longitude (approximately 9.27 × 10.30 km). Transects were steamed through the centres of these rectangles in an east–west direction (Figure 1), approximately perpendicular to the general orientation of the coastline, so tending to run across depth contours rather than parallel to them (MacLennan and Simmonds, 1991). Acoustic data were integrated over 5-min periods of passage along each transect, and 6–8 "samples" of 5 min were collected in each

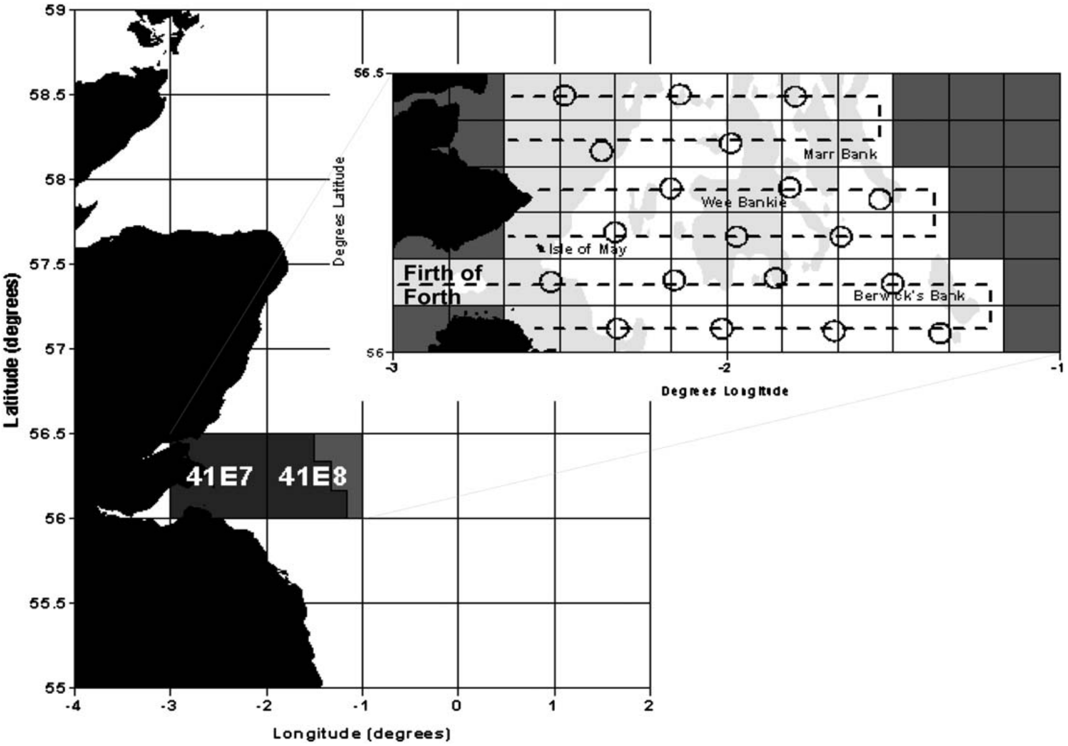

Figure 1. The location of the two ICES statistical rectangles that constituted the study area off the east coast of Scotland. The expanded section shows the division of the area into 50 rectangles of 5′ latitude by 10′ longitude, six main acoustic survey transects, and 19 demersal trawl stations. Light shading indicates regions of 50-m depth or less, and the locations of the main sandbanks are depicted. Heavy shading delimits the area included in the acoustic survey and demersal trawl biomass estimates.

Table 1. Dates and median Julian day when acoustic and demersal trawl surveys were carried out each year. The actual area covered by the acoustic survey in each year, and the raising factor required to equate the acoustic biomass estimates to that expected had the area covered in 1997 been covered in each subsequent year are also provided.

Year	Acoustic survey dates	Median Julian day (AS)	Area surveyed (km^2)	Raising factor	Demersal trawl survey dates	Median Julian day (DT)
1997	21–25 June	174	4721	1.0000	27 June–3 July	180
1998	13–16 June	165	3392	1.3918	18–22 June	171
1999	2–5 July	184	4645	1.0164	7–11 July	190
2000	14–19 June	167	4612	1.0236	20–24 June	173
2001	4–9 June	157	4671	1.0107	30 May–3 June	152
2002	15–19 June	168	4529	1.0424	9–13 June	162
2003	4–17 June	166	4529	1.0424	6–11 June	159

rectangle. Major concentrations of pelagic fish encountered during the course of each acoustic survey were sampled using an International Young Gadoid pelagic trawl fitted with a 6-mm codend (Figure 2A). The samples obtained were used to confirm species composition, to determine the size and age composition of the fish, and to determine sandeel length–weight relationships for each year. A 38-kHz split-beam transducer and a 120-kHz single-beam transducer were mounted in a towed body deployed forward of the propeller from a boom mounted near the bow of the vessel. The body, towed at a nominal speed of 18 km h^{-1} approximately 5 m below the sea surface, provided a more stable platform in rough weather and avoided the problems of interference from air bubble formation under the hull often associated with hull-mounted transducers. Only data from the 38-kHz transducer were used in the biomass estimation process. Although not ideal for sandeel discrimination, 38 kHz is certainly adequate, and the only sandeel target strength data available were obtained at this frequency (Armstrong, 1986). Sandeels provide a better acoustic return at higher frequencies, so data collected from the 120-kHz transducer were used to aid identification and discrimination of their shoals. Where there was doubt regarding the identity of the fish in a particular mark, the species composition in the appropriate pelagic trawl sample was used to attribute the integral values to species. Integral values for herring and sprat were assigned *pro rata* with their relative proportions (by weight) in the catch. This approach was considered inappropriate for assigning sandeel integrals because of their likely low catchability in the fishing gear compared with clupeids. Instead, if sandeels were caught in the trawl along with clupeids, both the 38-kHz and 120-kHz echo traces were re-examined to identify the marks most likely to consist of sandeels.

The 38-kHz transducer and echosounder were calibrated using a tungsten carbide sphere of known target strength suspended in the centre of the acoustic axis. The available target strength value for sandeels (TS, db kg^{-1} = −50) is independent of fish length; 1 kg of sandeels is assumed therefore to have a target strength of −50 db at 38 kHz no matter what size the fish are (Armstrong, 1986). Once surveyed, each transect's acoustic record was examined and the integral values obtained from the 38-kHz transducer for each 5-min run period were assigned to species. Knowing the target strength and identity of fish targets in the swath of water column ensonified by the acoustic pulse, the density (g m^{-2}) of sandeels present could be determined. For each rectangle of $5'$ latitude by $10'$ longitude, 6–8 density estimates, each the result of 5 min of survey, were obtained, and an overall estimate of the mean density of sandeels in the rectangle could be derived. Raising these by the area of sea in each rectangle provided estimates of sandeel biomass in each rectangle. Summing the results over all the rectangles, provided estimates of the total biomass of sandeels in the surveyed area during each cruise. In June 1998, poor weather conditions prevented the two most northerly transects from being surveyed. In 2000 and 2001, additional part-transects were steamed between the main transects over the major sandbanks or around the major seabird colony on the Isle of May (Figure 2A). Differences in the area actually covered by each survey needed to be taken into account in order to compare biomass estimates between years. The survey in 1997 covered the largest area. In subsequent years raising factors (RF_X) were determined to adjust the biomass estimate obtained in each year (X): $RF_X = Area_{1997}/Area_X$, where $Area_{1997}$ is the area covered in 1997 and $Area_X$ is the area covered in each of the other years (Table 1). Implicit in this is the assumption that the average density of sandeels in the area covered in each survey equalled the average density in the parts of the study area not covered. Trawl length frequency distribution data and survey weight-at-length relationships and age–length keys were used to break these biomass estimates down into particular size and age categories.

Acoustic survey techniques only detect sound returned from sandeel targets that are in the water column. Most of the sonar pulse is returned by the seabed, and the echosounder is incapable of quantifying sandeel biomass buried in the seabed. Consequently, biomass estimates obtained from the acoustic surveys were considered to be estimates only of the biomass of sandeels active in the water column.

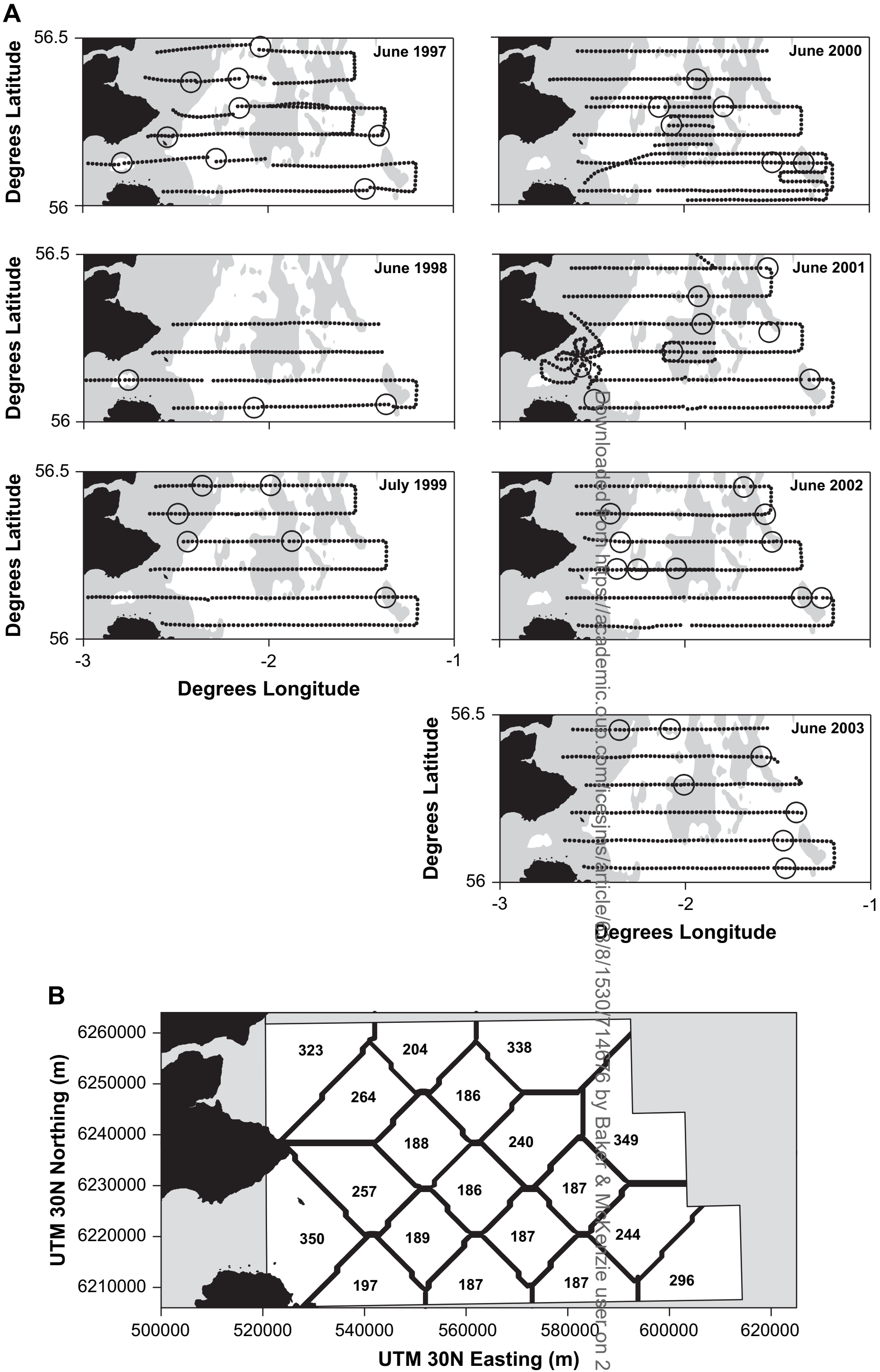

Figure 2. A. The actual acoustic survey track coverage in each year and the locations of the pelagic trawl sampling. B. The sea area associated with each demersal trawl station derived by "nearest neighbour" tessellation.

Demersal trawl survey

A Jackson rockhopper demersal trawl with a codend of 10-mm mesh was towed for 30 min at a speed of approximately 4 km h^{-1} at each of 19 evenly spaced sample stations (Figure 1). Net geometry monitoring equipment (SCANMAR, Norway) recorded the width and height of the trawl opening every 30 s. The ship's position, determined by Differential Global Positioning System (DGPS), was recorded simultaneously, so for each trawl sample, the area of seabed swept by the gear could be calculated. The total catch of sandeels in each trawl sample was quantified (number caught per 0.5-cm size class). Length-stratified subsamples were weighed to determine weight-at-length relationships and otoliths were extracted to determine age−length keys for each cruise. These were used to convert sandeel numbers at length to sandeel weight at length in each trawl. Dividing the number at length and weight at length of fish in each catch by the area of seabed swept by the trawl on each occasion converted these to density-at-length estimates (number km^{-2}, and kg km^{-2}). Multiplying the density-at-length estimates by the area of seabed associated with each trawl station determined by simple nearest-neighbour interpolation, or tessellation (Figure 2B), provided estimates of the total number and weight of sandeels, of each 0.5-cm length class, in each trawl station subarea. Summing these subarea population-at-length estimates across all trawl station subareas provided estimates of the total numbers and biomass at length of sandeels in the whole study area. Application of the age−length keys determined for each year enabled these estimates of total numbers and biomass at length to be assigned to the required age categories.

The low headline height of the demersal trawl (3.31 ± 0.06 m, $n = 133$) meant that only a small fraction of the water column was sampled on each deployment. However, the heavy contact of the ground gear on the seabed was likely to drive sandeels out of the sediment and into the path of the trawl (Meyer *et al.*, 1979; Hain *et al.*, 1995). Sandeel catches in heavy ground gear demersal trawls are higher at night when sandeels are buried in the sediment than by day when they are more active in the water column (Temming *et al.*, 2004). Consequently, the demersal trawl survey was considered primarily to provide an index of the biomass of sandeels in the sediment.

Nocturnal grab survey

A stratified random design was used for the nocturnal grab survey, in which sampling effort was disproportionately directed towards the sandy, silt-free habitats preferred by sandeels compared with the relative amount of such habitat within the study area (Holland *et al.*, 2005). Between 137 and 195 stations were sampled each year. At each station, a day grab sampling an area of 0.096 m^2 was deployed up to three times in order to obtain a single valid sample. Grab samples that contained less than 8-cm depth of sediment within the jaws were considered to be invalid in terms of estimating sandeel density. From each grab, sediment samples were extracted to determine whether the samples had been collected from suitable sediment types, insofar as sandeel habitat preferences were concerned. A detailed analysis of the relationship between sandeel density and size and sediment character revealed eight classes of sediment habitat. One of these habitat classes was considered to be unsuitable habitat for sandeels, and of the remaining seven habitat types, four were clearly preferred by sandeels (Holland *et al.*, 2005). Here we present sandeel density data by age for these four habitat types only. Sandeel density was determined by passing the sediment collected in each grab sample through a 5-mm mesh sieve to extract all sandeels. These were then counted, measured (to 0.5 cm below), weighed (to 0.1 g), and had their otoliths removed for age determination. Grab catches could therefore be quantified by both numbers and weight at both length and age. For further details of the grab-survey methodology and discrimination of the different habitat classes, see Holland *et al.* (2005).

The sandeel grab density data provided an index of the abundance of sandeels buried in the sediment at times of year and day when the entire population was likely to be buried in the sediment.

Cpue data

Off the Firth of Forth, sandeels are only fished by day from spring to early summer. Although the commercial industrial fishery in the area was closed from 2000 onwards, a limited experimental fishery was operated to allow the collection of the scientific data required by the Danish Institute of Fisheries Research (DIFRES) to monitor the sandeel population in the area. The cpue for a boat or a fleet is calculated by dividing the size of the catch, in weight or number of fish, by the amount of effort required to take the catch. Cpue is assumed to vary in proportion to variation in the abundance of the targeted fish population (King, 1995). For comparison with the fishery-independent survey data, the cpue data used in this study were extracted from logbook data for the Danish sandeel fishery operating on the Wee Bankie, Marr Bank, and Berwick's Bank (i.e. ICES statistical rectangles 41E7 and 41E8; Figure 1) over the period 1997−2003. The logbooks contain information about sandeel catches and fishing effort at the level of a fishing trip, in terms of catch weight and the number of days in which fishing took place within each ICES rectangle (30 × 30 nautical miles) visited. For each fishing trip, the trip median Julian day was determined from the Julian date of departure and the Julian landing date. Julian weeks were defined such that 1 January in each year (Julian day 1) was the first day of Julian week 1. Therefore, simply dividing each trip median Julian day by seven and rounding up allowed the trip to be assigned to a particular Julian week. The catch and effort information for all trips was in this way assigned to specific Julian weeks.

The pattern of fishing activity within the Danish sandeel fleet, in terms of vessel size, has changed over the years; the number of smaller vessels has decreased and the number of larger vessels has increased. Standardization of effort was required to compare catches and effort across all vessel size categories. Information about vessel size in the logbook data was provided in gross tonnage (GT) intervals of 10 GT for vessels up to 50 GT, and in 25-GT intervals for vessels >50 GT. Fishing effort for all vessels of any given gross tonnage ($\text{effort}_{\text{GT}}$) was therefore standardized to a 200-GT vessel equivalent (effort_{200}) using the equation

$$\text{effort}_{200} = \text{effort}_{\text{GT}} \frac{\text{GT}^b}{200^b},$$

where $b = 0.45$ and GT is the gross tonnage of the vessel concerned. Parameter b was estimated from:

$$\log(\text{cpue}_y) = a_y + b\log(\text{GT}),$$

where cpue denotes mean catch per unit effort (t d^{-1} fishing) for a trip, a_y denotes sandeel abundance in year y, and b denotes the standardization exponent for all years. For further details, see STECF (2004, 2005).

Preliminary examination of the Danish logbook data revealed that over the years 1997–2003, the main fishing activity in the study area was in Julian weeks 20–26 (20 May–7 July). To illustrate annual variation in fishing activity, catch and effort data were extracted for all trips with trip median Julian days falling within this 7-week period, and an annual cpue index was calculated. For a more direct comparison of the cpue index with the combined acoustic and demersal trawl survey estimates, catch and effort data were extracted for fishing trips with a median Julian day greater than or equal to the median Julian day of the first of these two surveys, and less than or equal to the median Julian day of the second of the two surveys (see Table 1), and again annual cpue indices were calculated.

The industrial fishery for sandeels uses large pelagic trawls that are prevented as far as possible from contacting the seabed for fear of sustaining gear damage. As a result, the fishery is unlikely to "sample" sandeels buried in the sediment. Commercial sandeel catches in the area consisted almost entirely of sandeels aged 1+ years (DIFRES, unpublished information). Cpue was therefore considered to provide an index only of the biomass of 1+ sandeels active in the water column.

1-D coupled biophysical model

Coupled biological and physical oceanographic modelling has advanced sufficiently in recent years so as to accurately capture important dynamics, such as the area-specific quantity of primary production, at temporal and spatial scales appropriate to the feeding behaviour of individual fish (Franks, 1992; Sharples, 1999; Waniek, 2003). These types of models, in particular the 1-D coupled biophysical model of Sharples (1999) and Sharples *et al.* (2006), can reproduce biologically important details of the vertical structure of the water column and the daily primary production, represented as chlorophyll concentrations for a given location. Biological information gained from this model, such as the annual timing of the spring bloom, has improved our understanding of local top predator population dynamics (Scott *et al.*, 2006). The physical component of the model, driven by local values for tidal forcing, surface heating, and surface winds, calculates for each day the vertical structure of currents, temperature, and light through the water column for the years in which the appropriate meteorological data are available. A turbulence closure scheme (Canuto *et al.*, 2001) is used to calculate the rates of turbulent mixing driven by tidal and wind stresses. The biological component calculates the response, in terms of chlorophyll concentration, of a single phytoplankton species to the light and nutrient environment, with the turbulent mixing controlling the vertical fluxes of phytoplankton and dissolved inorganic nutrients.

The tidal current data needed to parameterize the 1-D biophysical model for the study area were obtained from a hydrographic mooring located within the area at 56°15′N, 01°15′W, and a water depth of 65 m. The mooring provided information, at 10-min resolution, on the changes in vertical structure (at 5–10-m intervals), such that it was possible to define the depth of the surface mixed layer and the strength of the thermocline at any point in time. The mooring had two current meters, one fluorometer, and eight mini-loggers (temperature recorders), and operated from March to October of both 2001 and 2002. The temperature and fluorometry data obtained from the mooring were used to validate the model (Sharples *et al.*, 2006). The daily meteorological data, the daily mean values for solar irradiance, windspeed and direction, humidity, air temperature, and air pressure, needed to run the model for thermally stratified regions within the study area were collected at the Leuchars and Mylnefield Meteorological Stations in SE Scotland. These were obtained from the British Atmospheric Data Centre (BADC).

Results

Trends in fishing activity

As expected, catches in 1997 and 1998 were considerably larger than in any year during the closure period. However, in 1999 the catch was much less, despite the fishery being officially open (Figure 3). In fact, the scientific catch in 2001, when the fishery was closed, actually exceeded that taken in 1999. Given the small sample size, all data during the fishing period had to rank either higher or lower than all data in the closure period in order to obtain a significant Mann–Whitney test result. Simply considering the ranked annual landings in this way failed to produce a significant Mann–Whitney test comparing fishery years with closure years (Mann–Whitney $U = 1$, $p = 0.08$). Fishing effort

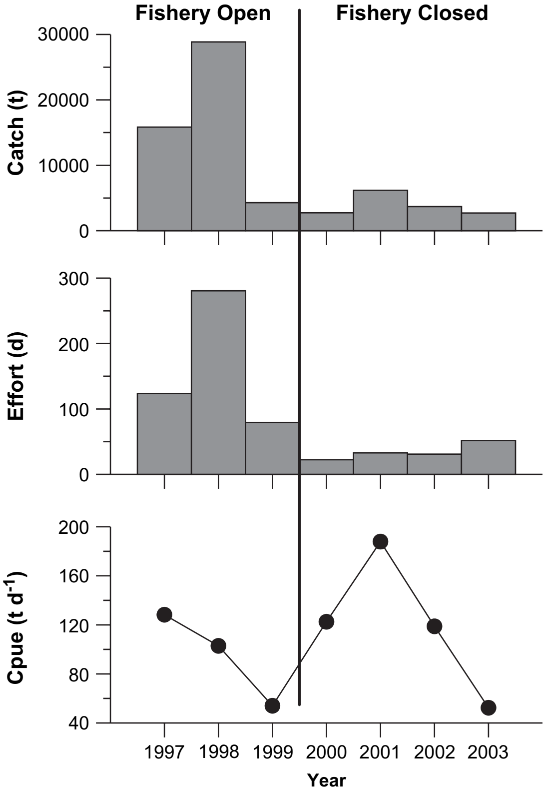

Figure 3. Annual variation in the Danish sandeel fishery, catch, effort, and cpue data for ICES statistical rectangles 41E7 and 41E8, determined for the period including Julian weeks 20–26.

was also lower in 1999 than in the two preceding years (Figure 3), but this was almost certainly a case of fishers responding to the unusually low cpue by stopping fishing. Fishing effort in all three fishery years was higher than in all four of the closure years (Mann–Whitney $U = 0$, $p = 0.03$), so closing the fishery certainly reduced fishing effort in the area. There was no indication from the cpue data to suggest that sandeel biomass in the area was any higher during the period of the moratorium than during the earlier period when the fishery was active (Figure 3; Mann–Whitney $U = 5$, $p = 0.72$).

Individual biomass index trends

Variation in the biomass/abundance of both 0-group and 1+ sandeels indicated by each assessment method is shown in Figure 4. None of the Mann–Whitney tests comparing fishery years with closure years were statistically significant. Even so, some suggestion of a recovery in the biomass of 1+ sandeels following the fishery's closure was apparent in the three fishery-independent survey trends. For both the demersal trawl and acoustic surveys, the lowest biomass estimate obtained during the closure years was lower than the highest biomass estimate obtained during the fishery years, sufficient to give a non-significant Mann–Whitney test result ($U = 1$, $p = 0.08$ for both indices). However, in both instances this was only just the case (Figure 4). The grab-survey density estimates obtained in 1998 and 1999 were lower than all four estimates obtained during the years of the closure, but the reduction in the sample size (no autumn grab survey was carried out in 1997) reduced statistical power to the point where even this result was not statistically significant ($U = 0$, $p = 0.06$). On the other hand, the cpue index calculated for the same period as the acoustic/demersal trawl surveys showed no indication of any major effect of the fishery closure on 1+ sandeel biomass ($U = 5, p = 0.72$). None of the three fishery-independent assessment methods indicated any effect of the fishery closure on 0-group sandeel biomass in the area.

Otherwise, consistency between the behaviour of the different index values was low; none of the correlation comparisons between the three fishery-independent assessment method abundance estimates of either 0-group or 1+ sandeels were statistically significant (Table 2). Only the two indices of 1+ sandeel biomass in the water column, acoustic survey and cpue calculated for the period coinciding with the acoustic/demersal trawl surveys, revealed temporal trends that were significantly correlated (Figure 4, Table 2; $r^2 = 0.74$, $p = 0.013$). Trends in cpue determined for the whole period (Figure 3) and for the period immediately coinciding with the combined acoustic/demersal trawl surveys (Figure 4) were similar ($r^2 = 0.77$, $p < 0.01$), but of course these two indices were not independent of each other. The acoustic survey biomass estimate was actually significantly correlated with both cpue indices, although the relationship was closer for cpue calculated for the period coinciding with the surveys ($r^2 = 0.74$, $p = 0.013$) than for the whole fishing season ($r^2 = 0.66$, $p < 0.03$).

Primary productivity passing through the food chain fuels the food supply to sandeels. Variation in the chlorophyll concentration in the water column, therefore, provides an indication of the "feeding opportunity" for sandeels. The 1-D coupled biophysical model was used to estimate the daily total water column chlorophyll concentration in each year (Figure 5). Integrating these curves up to the date of the combined acoustic demersal trawl survey in each year, i.e. the Cumulative water Column Chlorophyll Concentration (CCCC), provided an indication of the total "feeding opportunity" available to sandeels prior to each survey (Table 3). Timing of the combined acoustic/demersal trawl surveys in each year varied by 32 days, while the start date of the spring bloom varied by 16 days. As a result, the timing of the combined acoustic/demersal trawl survey relative to the start of the spring bloom varied by a factor of two, from as little as 38 days later in 2001 to as long as 76 days later in 1999 (Table 3). Consequently, the "feeding opportunity" available to sandeels prior to each survey, indicated by CCCC, varied by a factor of 1.6; from 9709 to 15 508 mg d m^{-2}. Perhaps a certain growth target or body condition level acts as a trigger, causing sandeels to cease feeding in the water column and enter the

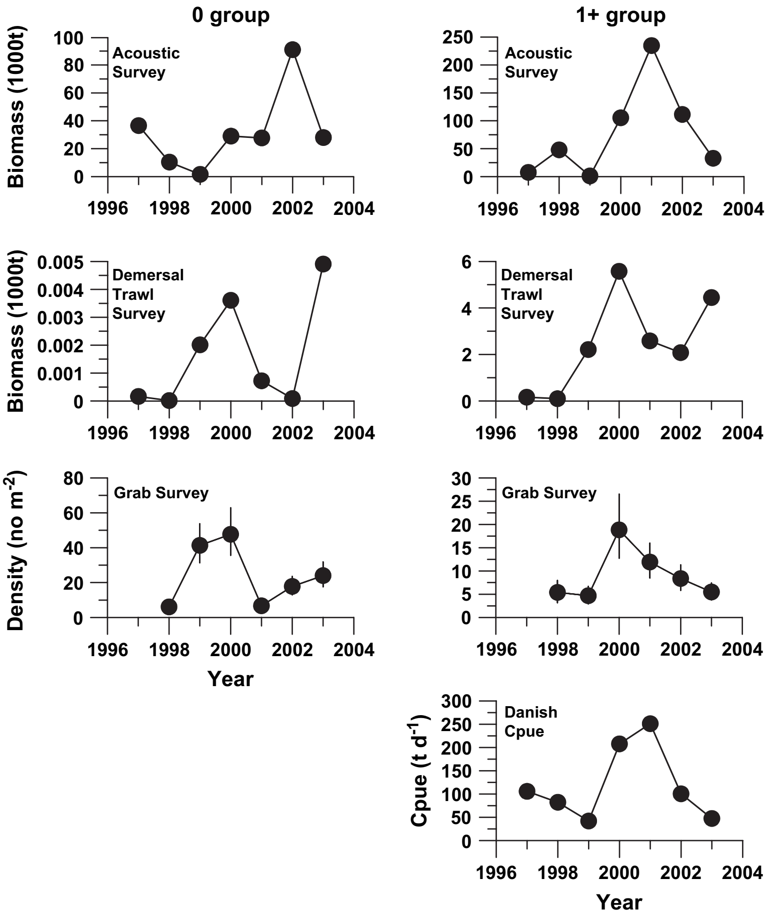

Figure 4. Between-year variation in the biomass/abundance of 0-group and 1+ sandeels indicated by three fishery-independent assessment methods (acoustic survey, demersal trawl survey, and autumn nocturnal grab survey) and fishery-dependent cpue data determined for the period immediately coinciding with the timing of the combined acoustic and demersal trawl surveys.

over-wintering phase of their life cycle buried in sediment (Winslade, 1974c). Then, such a variation in "feeding opportunity" could have led to considerable variation in the proportions of sandeels active in the water column or buried in the sediment at the times of the combined acoustic/demersal trawl surveys. Given that the different fishery-independent assessment methods sample sandeels in the water column and in the sediment to differing extents, the lack of significant correlations between them is therefore entirely to be expected.

As acoustic surveys only detect sandeels active in the water column, whereas demersal trawl surveys primarily sample sandeels buried in the sediment, these two biomass assessment methods are complementary. By taking account of sandeel emergence behaviour and reconciling the differences between the two indices, they can be combined to provide an index of total sandeel biomass in the area. The grab sampling carried out at night in autumn should have sampled the population at a time when all sandeels should have been buried in the sediment. This survey, therefore, also provides an index of total population abundance that can be used to verify the combined acoustic and demersal trawl survey estimate.

Development of a sandeel biomass model

1+ sandeels

The total biomass B_{TOT} of sandeels at a given time is the sum of the biomass in the water column (B_{WC}) and the biomass buried in the sediment (B_{SED}). The acoustic survey provides an estimate of the absolute biomass of sandeels in the water column (B_{AS}), so that $B_{\mathrm{AS}} = B_{\mathrm{WC}}$. We assume, as with any trawl survey or cpue index, that the demersal trawl survey index (B_{DT}) varies proportionally with variation in the biomass of sandeels in the sediment, so that $B_{\mathrm{DT}} = q_{\mathrm{DT}} B_{\mathrm{SED}}$, where q_{DT} is the catchability coefficient of the demersal trawl for sandeels (King, 1995). Thus,

$$B_{\mathrm{TOT}} = B_{\mathrm{AS}} + B_{\mathrm{DT}} q_{\mathrm{DT}}^{-1}. \tag{1}$$

From this it follows that at the time of each survey, the proportion of the total sandeel biomass buried in the sediment (P_{SED}) may be expressed as

Table 2. Results of correlation analyses comparing the temporal trends for each sandeel biomass/abundance index. Significant correlations are emboldened.

Age class	Biomass index comparison	r^2	p
0	Acoustic survey vs. demersal trawl survey	−0.076	0.550
	Acoustic survey vs. autumn nocturnal grab survey	−0.034	0.728
	Demersal trawl survey vs. autumn nocturnal grab survey	0.381	0.192
1+	Acoustic survey vs. demersal trawl survey	0.065	0.581
	Acoustic survey vs. autumn nocturnal grab survey	0.326	0.237
	Demersal trawl survey vs. autumn nocturnal grab survey	0.406	0.174
	Danish cpue vs. demersal trawl survey	−0.092	0.508
	Danish cpue vs. autumn nocturnal grab survey	0.397	0.180
	Danish cpue vs. acoustic survey	**0.738**	**0.013**

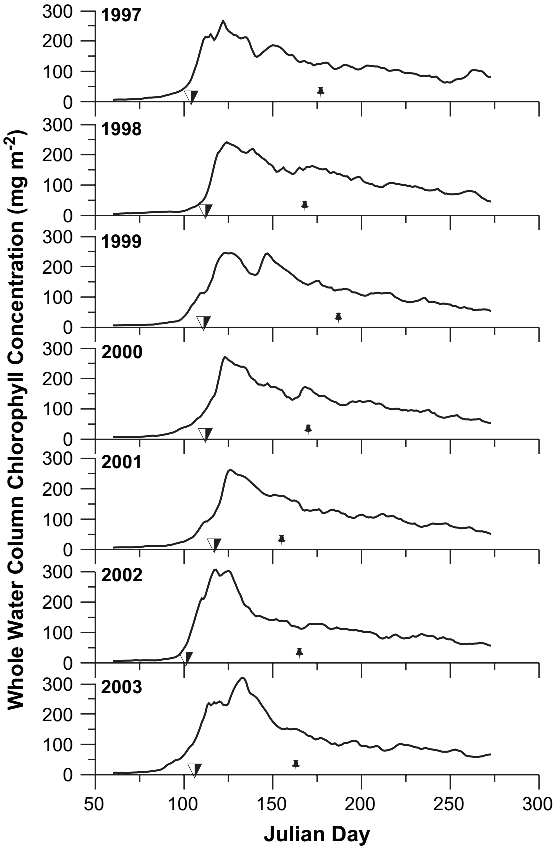

Figure 5. Daily variation in whole water column chlorophyll concentration throughout each of the years 1997–2003. The start of the spring bloom and the date of the combined acoustic and demersal trawl surveys in each year are indicated by inverted triangles and pin symbols, respectively.

$$P_{\mathrm{SED}} = \frac{B_{\mathrm{DT}} q_{\mathrm{DT}}^{-1}}{B_{\mathrm{AS}} + B_{\mathrm{DT}} q_{\mathrm{DT}}^{-1}}.$$

We posit that optimal sandeel behaviour requires 1+ sandeels to emerge to feed in the water column during a period when foraging is most profitable. However, while active in the water column, sandeels experience higher rates of mortality, principally through raised predation risk. The optimum life history strategy is therefore to keep the feeding period as short as possible to minimize mortality, but long enough to acquire sufficient energy reserves to reproduce and survive the ensuing non-feeding winter period. Therefore, as the feeding period progresses, with increasing cumulative opportunity to feed, an increasing number of sandeels will attain the body condition level required, terminate their feeding activity, and bury themselves in the sediment. As a proxy for this sandeel feeding opportunity we use the CCCC (C in our model), and indeed a significant fraction of between-year variation in the acoustic survey 1+ sandeel biomass was related to variation in CCCC over the period preceding each survey (Figure 6A). The logistic equation describes just such a gradual increase in the proportion P_{SED} of inactive sandeels in the sediment,

$$P_{\mathrm{SED}} = \frac{1}{1 + \exp(ab - bC)},$$

where a is the point of equal proportions in the sediment and the water ($P_{\mathrm{SED}} = 0.5$), and b is the rate of change from active to buried behaviour in the population equal to the slope of the regression of the logit transformed proportions vs. CCCC: $\ln(P_{\mathrm{SED}}/1 - P_{\mathrm{SED}}) = i + bC$ (logit transformations linearize the logistic equation and normalize errors). We therefore assume the following relationship:

$$\frac{B_{\mathrm{DT}} q_{\mathrm{DT}}^{-1}}{B_{\mathrm{DT}} q_{\mathrm{DT}}^{-1} + B_{\mathrm{AS}}} = \frac{1}{1 + \exp(ab - bC)}. \tag{2}$$

By rearranging and log-transforming Equation (2), we obtain the relationship

$$\ln\left(B_{\mathrm{DT}y}\right) - \ln\left(B_{\mathrm{AS}y}\right) = \ln(q_{\mathrm{DT}}) - ab + bC_y + \varepsilon_y.$$

Letting $\lambda = \ln(q_{\mathrm{DT}}) - \gamma$, where $\gamma = ab$, and $Y_y = \ln\left(B_{\mathrm{DT}y}\right) - \ln\left(B_{\mathrm{AS}y}\right)$, b and λ may be estimated by the linear regression of $Y_y = \lambda + bC_y$ for positive values of $B_{\mathrm{DT}y}$ and $B_{\mathrm{AS}y}$ (Figure 6B).

Given the estimate of $b = 0.0008919$, then a and $\ln(q_{\mathrm{DT}})$ remain linked within the derived value for $\lambda = -14.6356$. The range of reasonable values for q_{DT} is limited because a very small value would imply exceptionally poor catchability combined with no influence of the chlorophyll

Table 3. Julian dates of the combined acoustic/demersal trawl surveys, i.e. the Julian date of the day in port between the two surveys, and the start of the spring bloom, which is defined as the first day in which surface water chlorophyll concentration exceeded 2 mg m^{-3} for five consecutive days (after Scott *et al.*, 2006). The time span between these two dates is also shown together with the cumulative daily, whole water column, chlorophyll concentration over the part of each year preceding each annual combined survey.

Year	Julian day of combined acoustic/ demersal trawl survey	Julian day of start of spring bloom	Number of days between start of bloom and combined surveys	Cumulative daily whole water column chlorophyll concentration (mg d m^{-2})
1997	177	104	73	13 866
1998	168	112	56	10 959
1999	187	111	76	15 508
2000	170	112	58	12 412
2001	155	117	38	9 709
2002	165	101	64	12 948
2003	163	106	57	13 906

signal, whereas $q_{\mathrm{DT}} > 1$ indicates a concentration effect of the trawl. We considered a realistic interval, restricting catchability between $q_{\mathrm{DT}} > 0.0005$ and $q_{\mathrm{DT}} \leq 1$. The corresponding interval for a is then approximately 8000−16 500 (CCCC values). To find the most likely value of a within this interval that would also fit with other available information on the 1+ sandeel population, we used a linear correlation analysis to compare the total biomass of age 1+ sandeels estimated from the combined acoustic and demersal trawl surveys ($B_{\mathrm{TOT}y}$) with the grab-survey index ($B_{\mathrm{G}y}$), where $B_{\mathrm{TOT}y} = B_{\mathrm{DT}y}q_{\mathrm{DT}}^{-1} + B_{\mathrm{AS}y}$, allowing q_{DT} to vary with variation in a over the range of CCCC values 8000−16 000 mg d m^{-2}, according to the relationship $q_{\mathrm{DT}} = \exp(\lambda + ab)$. The curve describing the correlation coefficient for the linear relationship between $B_{\mathrm{TOT}y}$ and $B_{\mathrm{G}y}$ was dome-shaped over this range of values of a, with a maximum $r^2 = 0.674$ ($p = 0.045$) at an intermediate value of $a = 12\,045$ (Figure 6C). Figure 6D shows the actual relationship between B_{TOT} and B_{G} obtained using a value of a of 12 045. This optimal solution for a gives an estimate of the catchability of 1+ sandeels in the demersal trawl of $q_{\mathrm{DT}} = 0.0204$. Applying these optimal solutions for q_{DT} and a first to Equation (2) and then to Equation (1) allows variation in the proportion of 1+ sandeels buried in the sediment with increasing CCCC to be modelled (Figure 6E), and provides an estimate of total 1+ sandeel population biomass in each year as the sum of the fractions active in the water column and buried in the sediment (Figure 6F). Error bars in Figure 6F indicate the range of 1+ sandeel biomass predicted by the model over the range of values of a that gave a statistically significant r^2 in Figure 6C. The sandeel biomass model indicated that 1+ sandeel biomass in all the four years that the fishery was closed exceeded the biomass present in the area during the three years that the fishery was commercially active (Mann−Whitney $U = 0$, $p = 0.03$).

0-group sandeels

A similar approach was adopted to model the biomass of 0-group sandeels based on the combined acoustic survey and demersal trawl 0-group sandeel biomass indices such that Equations (1) and (2) were again considered to represent the situation. However, important differences in the biology of 1+ and 0-group sandeels necessitated some modifications to certain aspects of the model and caused some problems with parameter estimation. First, 0-group sandeels metamorphose from the larval stage in late May (Wright and Bailey, 1996); here, we assume a metamorphosis date of Julian day 145. Prior to this date, zooplankton production fuelled by primary productivity, as indicated by CCCC, would not be utilized by post-metamorphosis 0-group sandeels. Consequently we recalculated a CCCC value more appropriate to 0-group sandeels, the Cumulative total water Column Chlorophyll Concentration from Julian day 145 onwards (CCCC$_{145}$). Second, the length of 0-group sandeels immediately following metamorphosis is approximately 4.5 cm (Wright and Bailey, 1996). In the Firth of Forth, 0-group sandeels appear to need to attain a length of 7.5−8.0 cm before burying in the sediment (Holland *et al.*, 2005; GJH and SPRG, unpublished data), which at published growth rates would require 80 days or more (Wright and Bailey, 1996) leading to burial at around Julian day 225, i.e. mid-August. It was likely therefore that a large proportion of the 0-group sandeel population would have remained active in the water column at the time that the combined acoustic and demersal surveys were carried out in all the years that our study was conducted (Figure 5, Table 3). The lack of a significant relationship between the acoustic survey index and CCCC$_{145}$ tended to confirm this (Figure 7A). The polynomial fit, excluding the 2002 datum, driven by the low value acoustic biomass estimate obtained in 1999 when the survey was carried out latest in the year and at its highest CCCC$_{145}$ value, suggests that 0-group sandeels remained active in the water column until CCCC$_{145}$ exceeded at least 5000 mg d m^{-2}. This caused problems in estimating both b and a_{145} parameters, because many of the data points lay in the region where $P_{\mathrm{SED}} \approx 0$. Therefore, although regression of $Y_y = \lambda + bC_y$ provided estimates of $b = 0.0007921$ and $\lambda = -13.808412$, the regression was not statistically significant (Figure 7B). Moreover, a zero value demersal trawl index in 1998 provided an additional problem, because positive values were required from both indices in order to perform the analysis. Excluding that year's data from the analysis would have meant also discarding the perfectly valid 1998 acoustic survey information. To avoid this, we arbitrarily assigned a value of 0.000016 as the 1998 demersal trawl index value,

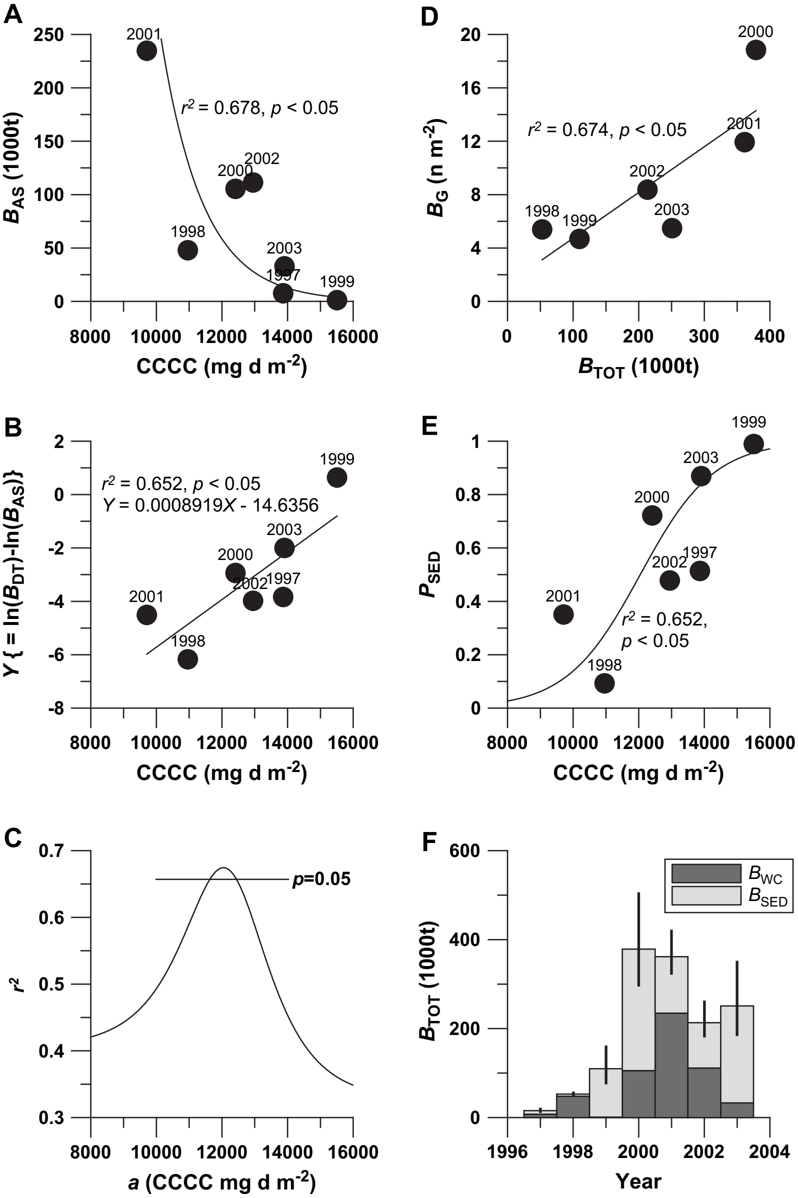

Figure 6. 1+ sandeel model. A. The relationship between the acoustic survey biomass estimate and CCCC. B. Linear regression of CCCC on Y to estimate b and λ parameters, where $Y_y = \ln(B_{DTy}) - \ln(B_{ASy})$, and b and λ are the slope and constant, respectively, of the regression analysis. C. The relationship between r^2 values of the correlation between the modelled estimate of 1+ sandeel biomass and the autumn grab-survey estimate of 1+ sandeel density as the value of the a parameter was varied. D. The best fit correlation between the modelled estimate of 1+ sandeel biomass and the autumn grab-survey estimate of 1+ sandeel density obtained at $a = 12\,045$. E. The modelled variation in the proportion of 1+ sandeels buried in the sediment with increase in CCCC, showing fit to the data. F. The annual variation in the modelled estimate of 1+ sandeel biomass, both in the water column and in the sediment. Bars indicate the range of modelled biomass in the sediment for the range of a values that gave a significant r^2 in panel C.

i.e. one-hundredth of the mean of all seven demersal trawl, 0-group sandeel, biomass indices.

Because in most years, 0-group sandeels remained active in the water column well after the combined acoustic/demersal trawl surveys have taken place, predation and other density-dependent processes would have continued to operate to reduce their abundance. As a result, the relationship between modelled sandeel biomass in June and July and the observed densities in the following autumn grab survey used to fix the value for a in the 1+ sandeel model would, in the case of 0-group sandeels, have been decoupled. Instead, we posit that the difference between

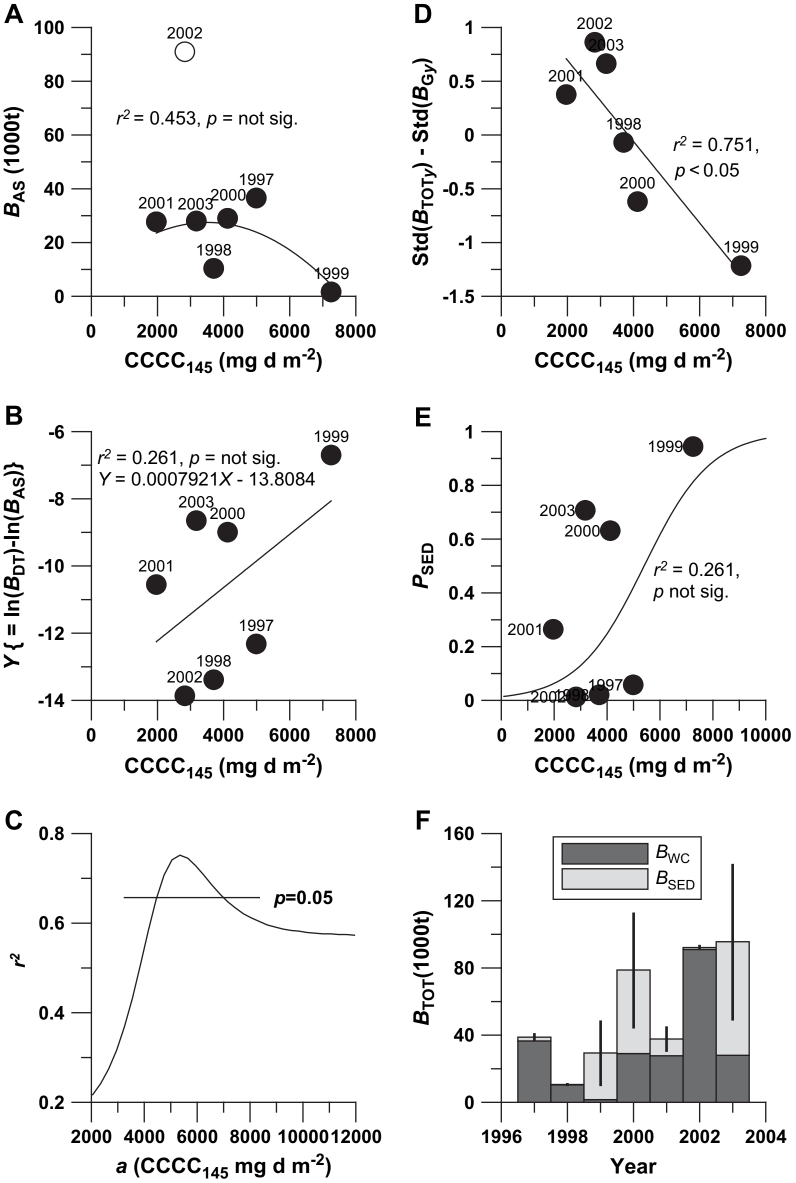

Figure 7. 0-group sandeel model. A. The relationship between the acoustic survey biomass estimate and $CCCC_{145}$. B. Linear regression of $CCCC_{145}$ on Y to estimate b and λ parameters, where $Y_y = \ln(B_{DTy}) - \ln(B_{ASy})$, and b and λ are the slope and constant respectively of the regression analysis. C: The relationship between r^2 values of the correlation between the difference between the standardized modelled estimate of 0-group sandeel biomass and the standardized autumn grab-survey estimate of 0-group sandeel density ($\mathrm{Std}B_{\mathrm{TOT}y} - \mathrm{Std}B_{\mathrm{G}y}$) with $CCCC_{145}$, as the value of the a_{145} parameter was varied. D. The best fit correlation between $\mathrm{Std}B_{\mathrm{TOT}y} - \mathrm{Std}B_{\mathrm{G}y}$ and $CCCC_{145}$ obtained at $a_{145} = 5400$. E. The modelled variation in the proportion of 0-group sandeels buried in the sediment with increase in $CCCC_{145}$ showing fit to the data. F. The annual variation in the modelled estimate of 0-group sandeel biomass, both in the water column and in the sediment. Bars indicate the range of modelled biomass in the sediment for the range of a_{145} values that gave a significant r^2 in panel C.

the two abundance estimates should be inversely proportional to the $CCCC_{145}$ at the time of the acoustic/demersal trawl surveys. If the acoustic/demersal trawl surveys took place early in the season (low $CCCC_{145}$), modelled 0-group sandeel biomass at this time should be higher relative to the grab-survey index than would be the case in years when the acoustic/demersal trawl surveys occurred later in the season (higher $CCCC_{145}$), because any population-reducing processes would have had longer to operate.

We tested this hypothesis over a range of a_{145} corresponding to $q_{\mathrm{DT}} = 0.000005$ to $q_{\mathrm{DT}} = 0.02$, assuming that 0-group sandeel catchability in the demersal trawl gear would in all likelihood be lower than the catchability of 1+ sandeels. For each value of a_{145} and q_{DT}, we determined the resulting modelled 0-group sandeel total population biomass and standardized these data ($\mathrm{Std}B_{\mathrm{TOT}y}$) by dividing the modelled biomass in each year ($B_{\mathrm{TOT}y}$) by the mean of the modelled biomass in all years ($\overline{B}_{\mathrm{TOT}}$). The grab-survey data were standardized in the same way ($\mathrm{Std}B_{\mathrm{G}y} = B_{\mathrm{G}y}/\overline{B}_{\mathrm{G}}$). We then carried out a linear correlation analysis to examine how the relationship between $\mathrm{Std}B_{\mathrm{TOT}y} - \mathrm{Std}B_{\mathrm{G}y}$ and CCCC_{145} varied with increase in a_{145} (Figure 7C). The best fit correlation (Figure 7D), obtained at $a_{145} = 5400$ (Figure 7C), provided an optimal estimate of $q_{\mathrm{DT}} = 0.0000726$, but the correlation r^2 was significant over the range $a_{145} = 4750$ to $a = 6850$, corresponding to $q_{\mathrm{DT}} = 0.0000434$ to $q_{\mathrm{DT}} = 0.0002288$. These values of a_{145} and q_{DT} were substituted in Equations (2) and (1) to model variation in the proportion of 0-group sandeels in the sediment with increasing CCCC_{145} (Figure 7E), and to estimate the total 0-group sandeel biomass present each year at the time of the combined acoustic/demersal trawl surveys (Figure 7F). The error bars in Figure 7F indicate the range of 0-group sandeel biomass predicted by the model over the range of a_{145} values that gave statistically significant r^2 in Figure 7C. Modelled 0-group biomass in three of the four fishery-closure years was higher than in the preceding three years when the fishery was in operation, giving a Mann–Whitney test that was not quite statistically significant ($U = 1$, $p = 0.08$).

Discussion

Closing fisheries to protect overexploited stocks is a well established fisheries management option (Pauly *et al.*, 2002). It is likely to be particularly successful with short-lived species with high recruitment potential (Gell and Roberts, 2003; Sale *et al.*, 2005), such as sandeels. On a previous occasion where closure of a sandeel fishery was initiated to protect stocks around Shetland, the local population size increased substantially within just a few years of the start of the moratorium (Wright, 1996; ICES, 2002). The main purpose of this paper has been to establish what effect a more recent sandeel fishery closure has had on a sandeel population off SE Scotland. In the past, the information used to monitor changes in sandeel stock size has generally originated from the fisheries themselves. Such data will invariably be available, given the need for active management of fisheries required under the Common Fisheries Policy. However, with the exception of the Shetland sandeel stock, any assessment of sandeels in the North Sea has to date been carried out at a whole North Sea scale, despite indications that sandeels in the North Sea almost certainly consist of several separate sub-populations (Proctor *et al.*, 1998; Pedersen *et al.*, 1999). Individual, age-based stock assessments at this local population scale have yet to be undertaken on a regular basis, and it is not certain that the data are available that would allow this to be done with adequate precision from a management perspective (Lewy *et al.*, 2004). This is regrettable, because the distribution of one of these local sandeel populations underpinned the demarcation of the sandeel fishery closure area off SE Scotland, and such an assessment would perhaps have provided the best indication of the impact of the management action on the local sandeel stock.

At present Denmark holds, by some considerable margin, the largest North Sea sandeel quota. Logbook data provided by Danish fishers allowed variation in cpue on the fishing grounds off SE Scotland to be examined. In the absence of such a fishery, no fishery-dependent assessment methods would be applicable for monitoring the effects of management through fisheries moratoria. Therefore, if fishery-dependent data underpin the advice that culminates in decisions to close fisheries, maintenance of these data time-series will require some form of scientific or experimental fishery to be contained to provide the information required to monitor the effectiveness of fishery closures. This would be particularly critical if the data collected while a fishery was in operation provided some sort of reference point that was to be used to inform future decisions to re-open fisheries. In the case of the sandeel fishery closure off SE Scotland, such data were only available for the period of the closure, because a strictly limited scientific fishery was continued throughout. The implication is that it could be very difficult for managers to impose complete closures of fisheries.

While closure of the sandeel fishery certainly reduced fishing effort in the area, the effect on catches was less clear-cut. The catch in 1999, the last year that the commercial fishery was open, was in fact very much on a level with catches by the scientific fishery during the four closure years. Only in 1997 and 1998 were catches substantially higher. The cpue in 1999 was considerably lower than in the two preceding years, indicative of a much lower 1+ sandeel biomass in the area. It is possible that this low cpue was not economically viable, forcing fishers to abandon fishing activity in the area in the last year before closure. Variation in cpue calculated over the entire season in each year suggested no major recovery in the 1+ sandeel stock following closure of the fishery, and the same was true for a cpue index determined for the period immediately coinciding with the combined acoustic and demersal trawl surveys. Trends in the biomass of both 0-group and 1+ sandeels derived from three fishery-independent stock assessment methods were also examined. Two of these assessments, the acoustic survey and the demersal trawl survey, were carried out in early summer, at approximately the same time of year as the main fishery. The third method, the nocturnal grab survey, was undertaken in autumn of each year. Like the two cpue indices, none of these fishery-independent methods indicated a clear-cut response of either age class of the sandeel population to the fishery closure, although in the case of 1+ sandeels, all three fishery-independent assessments tended to suggest that there may have been one.

For neither age group did the fishery-independent indices vary consistently over time. Sandeels spend most of their time buried in the sediment, emerging briefly to spawn in mid-winter and again in late spring/early summer to feed on the burst of zooplankton production triggered by the annual plankton bloom (Macer, 1966; Winslade, 1974c; Gauld and Hutcheon, 1990; Bergstad *et al.*, 2001). This characteristic of moving between the seabed sediment and the overlying water column almost certainly explained the inconsistency between the three assessment methods, each of which detected sandeels in the two parts of the marine environment to a greater or lesser extent. Danish cpue and the acoustic survey provided an index of variation in the biomass of 1+ sandeels in the water column; that these two indices should provide the only significant correlations provided strong support for this contention. Moreover, because the proportion of sandeels active in the water column is likely to vary over time, the closer relationship between the acoustic survey index and cpue calculated for the period coincident with the combined acoustic/demersal trawl survey, rather than with cpue calculated over the whole season, further supports this argument.

Although the need to emerge in winter to reproduce is a prerequisite for the continued survival of the species, the strategy by which individual sandeels reach this critical point is much more elective. Like many other organisms subject to high predation mortality, sandeels have to balance the need to obtain food against the need to reduce predation risk (Lima and Dill, 1990). When foraging exposes animals to predation risk they should forage for the minimum time possible and then return to refugia (Pearson *et al.*, 1984). Although not totally immune from predators while buried (Girsa and Danilov, 1976; Hobson, 1986; Temming *et al.*, 2004), it is widely assumed that the seabed sediments provide such a refuge (Reay, 1970). It is during late spring and early summer, when sandeels are most active in the water column, that they feature most strongly in the diets of many fish, seabird, and marine mammal predators (Bailey *et al.*, 1991; Greenstreet *et al.*, 1998; Brown *et al.*, 2001).

If sandeels are most vulnerable to predation while active in the water column, then during the feeding period of late spring to early summer, they should feed only for so long as is necessary to achieve an adequate body condition to ensure their survival through winter and to meet their gonad production requirements. Once these objectives are met, sandeels increase their chances of survival by returning to the sediment and reducing their risk of mortality from predation. Winslade (1974c) suggests that this is indeed the case, i.e. once sandeels attain a "certain fat content", the over-wintering phase of their life cycle is triggered, causing them to cease feeding in the water column. Certainly the period that sandeels are active in the water appears to be relatively short. Commercial pelagic catches start to increase in April, peak in June, then decline in July (Macer, 1966; Winslade, 1974c; Reeves, 1994). The increase in commercial landings closely tracks the increase in copepod abundance early in the season (Winslade, 1974c), consistent with the observation that emergence only takes place when prey are available in the water column (Winslade, 1974a). In July, however, sandeel landings decline at a much faster rate than expected given the slower decline in copepod abundance (Winslade, 1974b). Somatic growth of sandeels is also highly seasonal, being strongest from March to June and almost ceasing in 1+ sandeels by July (Bergstad *et al.*, 2002). Meeting the increased costs of metabolism associated with the continuing rise in sea temperature into July and August appears to inhibit continued growth. Without the benefit that further increase in body size and condition might endow, the risk from predation associated with continued feeding in the water column would appear to be sufficient to cause sandeels to cease feeding and to bury in the sediments, once they have reached an adequate condition to survive winter. In Japanese waters a slightly different situation exists, but a similar logic applies. Rising seawater temperatures cause a closely related species, *Ammodytes personatus*, to cease feeding and to aestivate in the sediment in order to conserve energy. With increasing temperature, larger sandeels within an age class enter into an aestivation state before smaller fish do, indicating the importance of fat reserves as a stimulus (Tomiyama and Yanagibashi, 2004). Previous studies had also demonstrated that the more opportunity these sandeels had had to feed, the earlier they started to aestivate (Yanagibashi *et al.*, 1997; Yamada *et al.*, 1999).

As the feeding period progressed, the proportion of the sandeel population active in the water column in our study area is likely to have declined while the proportion buried in the sediment would have increased. Consequently, the different assessments undertaken in late May or early June would have been affected not only by the variation in total sandeel biomass, but also by differences in the proportions of the population in the water column and in the sediment. Thus, for example, 68% of variation in the acoustic survey index of 1+ sandeel biomass could be explained by variation in CCCC, a proxy for the total feeding opportunity available to sandeels prior to each of the combined acoustic/demersal trawl surveys. By combining the information provided by two complementary assessment methods carried out at the same time of year, acoustic and demersal trawl surveys, a model was developed to estimate the total biomass of each sandeel age class in the study area at the time of the combined surveys.

The model assumes that the acoustic survey provides an estimate of the absolute abundance of sandeels in the water column. If we consider the acoustic survey in the same way that we have used the demersal trawl survey, i.e. $B_{\mathrm{AS}} = B_{\mathrm{WC}} q_{\mathrm{AS}}$, then we have in effect assumed that $q_{\mathrm{AS}} = 1.0$. This may not be the case. It is possible that other reflecting targets have been mis-classified as sandeels, leading to q_{AS} values >1.0 or alternatively that sandeels have been mis-classified as something else, leading to q_{AS} values <1.0. These potential errors may tend to cancel each other out. However, because assessment of the echo-integral records was undertaken by the same two considerably experienced scientists (SPRG and EA) in each year, there may be a greater potential for bias, in that the same errors were likely to be consistently made in each year. In many ways, this is the preferable case, because a consistent bias means that, if later found necessary, an acoustic survey q_{AS} parameter can be added to revise the model output accordingly. Recent and continuing work to develop an objective algorithm to assign echo-integral data to sandeel and other fish or plankton categories indicated close agreement with the subjective, experience-based method used here (Mosteiro *et al.*, 2004). The model further assumes that the demersal trawl index varies as a linear function of the biomass of sandeels buried in the sediment, such that $B_{DT} = B_{SED}q_{DT}$, where q_{DT}, the catchability coefficient of sandeels in the demersal trawl, is constant. In this study, the same demersal trawl was fished by the same officers and crew operating the same research vessel each year. Moreover, the Jackson rockhopper trawl had been in use for many years prior to this particular study, so no element of learning was involved early in the study. Furthermore, the same 19 stations were fished each year, so the probability of sampling specific sandeel habitats should have remained constant. Hence, variation in the area actually swept by the gear each year was the only source of between-survey variation in effort, but this was taken into account in the formulation of the demersal trawl biomass index. The demersal trawl survey, therefore, violated none of the assumptions underpinning this relationship (King, 1995), so there was no reason to believe that the sandeel catchabilty coefficient for the Jackson rockhopper trawl was not constant across all surveys.

The model states that total sandeel biomass in the area is the sum of sandeel biomass in the water column and sandeel biomass in the sediment (Equation (1)), and that the proportion of sandeel biomass buried in the sediment varies as a logistic function of CCCC prior to the combined acoustic/demersal trawl surveys (Equation (2)). By determining values of the *a* and *b* parameters for the logistic curves describing the burial behaviour of each sandeel age class, estimates of the catchability coefficients of both 1+ and 0-group sandeels in the demersal trawl could be derived. For 1+ sandeels this was straightforward. The linear regression used to determine *b* was statistically significant. Comparison of the various modelled 1+ sandeel biomass estimates with the grab-survey 1+ sandeel abundance index, because both *a* and q_{DT} were allowed to vary over a predefined range of possible values, was straightforward and provided a relatively limited range of *a* values giving a significant correlation. Applying the determined value for *b* and the optimal solution for *a* in Equation (2) produced a logistic curve of variation in the proportion of sandeel biomass in the sediment with increasing CCCC prior to each combined survey that was a significant fit to the observed data. Using the range of values of *a* giving a significant correlation between the modelled biomass and the grab index to provide a range of possible q_{DT} values to apply in Equation (1) had a negligible effect on the ranked order of each year's modelled 1+ sandeel biomass. No matter which value of *a* and associated q_{DT} was used, our estimates of 1+ sandeel biomass derived from the model suggested that the biomass in all four years that the fishery was closed was higher than in any of the preceding three years when the fishery was operating, a result that produced a significant Mann–Whitney test result.

Modelling 0-group sandeel biomass was more problematic. First, the *b* parameter could not be determined with any great confidence because the linear regression used to estimate it was not statistically significant. Second, because of differences in the biology of 1+ and 0-group sandeels, CCCC values cumulated from a more appropriate start date had to be calculated, and an alternative hypothesis relating modelled 0-group biomass to the 0-group grab-survey index had to be employed. Significant correlations were obtained, but over a relatively wide range of possible values of *a* and associated estimates of q_{DT}. As a result, the logistic curve describing variation in the proportion of 0-group sandeel biomass buried in the sediment as a function of CCCC failed to provide a significant fit to the observed data. The range of possible q_{DT} values was such that the modelled estimate of 0-group sandeel biomass buried in the sediment was considerable, sufficient to affect the ranked order of each year's estimate of total biomass. Over the full range of possible *a* and associated q_{DT} values, the same three years, 2000, 2002, and 2003, were always ranked 1–3 (highest biomass). Therefore, whichever value of q_{DT} was applied, modelled 0-group biomass was higher in three of the four fishery-closure years than in each of the preceding three years when the fishery was in operation, a result that failed to produce a significant Mann–Whitney test result. The remaining fishery-closure year was always ranked fifth, being beaten by either 1997 or 1999, depending on the value of q_{DT} used.

The problems experienced in modelling 0-group sandeel biomass almost certainly reflect major differences in the processes that influence 0-group and 1+ sandeel feeding and burial behaviour. While our model appears to have captured the situation regarding 1+ sandeel reasonably well, this appears not to be the case with respect to 0-group sandeels. Numerous factors may affect 0-group sandeel behaviour that at present our model cannot take into account. In determining the parameters *a* and *b* of the logistic function we only have one datum for each year. We use all seven years of data to estimate these parameter values, and in doing so we make the assumption that the shape of the curve and its position relative to CCCC is constant over all years. Although this assumption appears to have held reasonably well for 1+ sandeels, there are clear indications that this was not the case for 0-group sandeels. There may be several reasons for this. Variation in mean egg-hatch date between years in turn leads to differences in the timing of metamorphosis from the larval phase (Wright and Bailey, 1996). In our study, we assumed a constant metamorphosis date of Julian day 145 in determining the CCCC values appropriate to 0-group sandeels. Variation in the date of metamorphosis would, in effect, alter the location of the logistic curve describing the proportion of 0-group sandeels in the sediment; effectively altering the *a* parameter of the model. Sandeel growth rates display density-dependence, being lower in years of particularly high cohort strength (Bergstad *et al.*, 2002). In 2002, the acoustic survey estimate of 0-group biomass was higher than in any other year, by a factor of three. This may have impeded growth rates so that, by the time of the survey, the sandeels may not have reached the body size and condition expected given the feeding opportunity apparently available to them. Some studies have suggested a negative density-dependent relationship between 0-group and older sandeels (Arnott and Ruxton, 2002; Furness, 2002). Therefore, in years when 1+ sandeel biomass was elevated, high densities of these older fish in the sediment may have inhibited the burial behaviour of 0-group sandeels. Such factors may well have affected the slope of the logistic curve, altering the *b* parameter, as well as the curve's location relative to CCCC.

The 0-group acoustic survey data suggested that 0-group sandeels remained active in the water column later in the year, and at higher CCCC values, than 1+ sandeels. The metamorphosis dates and growth rate information published by Wright and Bailey (1996) suggest that this was likely, and it is consistent with the observations that 0-group sandeels continue to be caught in the pelagic trawls used by the industrial fishery (Macer, 1966; Winslade, 1974c; Reeves, 1994), and to continue to increase body condition (Bergstad *et al.*, 2002), much later in the year than their older conspecifics. Winslade (1974c) suggested that older sandeels have slower growth rates, so they reach their fat-level thresholds and cease activity in the water column earlier than younger fish. Consequently, older sandeels generally spend less time in the water column (Kvist *et al.*, 2001). Similarly, in Japan, 0-group *A. personata* remained active in the water column longer and started aestivation later than older fish (Tomiyama and Yanagibashi, 2004). This tendency for 0-group sandeels to remain in the water column later in the year may also have contributed to the greater difficulty in parameterizing the 0-group model. Timing of the combined acoustic/demersal trawl surveys was opportune for estimating *b* in the 1+ sandeel model. The data were distributed across a range of CCCC, and related biomass proportions in the sediment, that was ideal for the linear regression analysis. This was less so for 0-group sandeels. At the time of year that the surveys were generally carried out there was a greater tendency for data to be collected at CCCC values well below the value of the *a* parameter, and with low biomass proportions in the sediment, a data distribution that was not conducive to satisfactory linear regression.

The approach to modelling 0-group sandeel biomass needed revision to take account of the fact that 0-group sandeels remained active in the water column sometimes well after the combined acoustic and demersal trawl surveys were completed. In such circumstances, 0-group sandeels would have been prone to greater and continued mortality from predation (Temming *et al.*, 2004; Greenstreet, 2006). Therefore, we had no reason to expect a straightforward relationship between modelled 0-group biomass and the later grab-survey estimates of 0-group sandeel population density. Instead, we proposed that the difference between these two population size estimates, subtracting the standardized grab-survey index from the standardized modelled biomass, was inversely proportional to variation in CCCC, and this was indeed the case.

Three final points are worthy of some consideration. First, the model we apply here effectively tunes the demersal trawl estimates of sandeel biomass in the sediment to the acoustic survey. Therefore, the choice of target strength used in the analysis of the acoustic integral data is critical. Consequently, while the modelled biomass estimates may certainly be considered as estimates of relative biomass, their use as estimates of absolute abundance is critically dependent on the sandeel target strength of -50 db kg^{-1} used here. Armstrong (1986) suggests that sandeel target strength lies within the range -46.9 to -54.7 dB kg^{-1} at 38 kHz. A 3 dB kg^{-1} difference from the target strength used here, i.e. -47 dB kg^{-1}, would result in a halving of our absolute biomass estimates. The relative proportions in the sediment and in the water column predicted by the model would be unchanged, so changes in relative biomass predicted by the model would also remain unaffected by this increase in target strength. Second, by the Julian day of the combined acoustic and demersal trawl surveys in 1997 and 1998, approximately 65% and 90% of the total catches of 16 200 t and 29 300 t of sandeels, respectively, had already been taken by the fishery (HJ and HM, unpublished data). In effect, therefore, in 1997 approximately 10 530 t and in 1998 approximately 26 370 t of sandeels present earlier in the season were not accounted for by the model. In 1999, the sandeel fishery was over by the time the surveys took place, but in that year landings only amounted to 4000 t, so the effect was much reduced. Similarly, in all subsequent years, the fishery was officially closed and scientific landings never exceeded 6500 t, a very small fraction of the modelled biomass in each year. A detailed analysis of seasonal variation in fishery cpue data in relation to the modelled sandeel emergence behaviour is planned for the future. Third, the catchability of 0-group sandeels in the demersal trawl (0.000073) was two orders of magnitude lower than that of 1+ sandeels (0.0204). The demersal trawl simply did not sample 0-group sandeels well.

As 0-group sandeels spend a longer period in the water column, acoustic surveys may instead provide the best assessment of the biomass present in an area in a particular year, particularly if these surveys could be consistently undertaken relatively early in the year, when CCCC is still relatively low, and the proportion of 0-group sandeels likely to be buried in the sediment is small.

The industrial sandeel fishery that operated off SE Scotland targeted 1+ sandeels almost exclusively, in common with the North Sea sandeel fishery generally (Gislason and Kirkegaard, 1998; Kvist *et al.*, 2001). Therefore, it might be expected that this age class should respond to the fishery closure, and the model results confirm that this was the case. In fact 1+ sandeel biomass increased markedly in 2000, the first year of the closure, when perhaps a lag of one or two years might have been anticipated to allow successive recruitment to build stocks. No such lag was apparent because, although allowed, very little fishing actually took place in the area in 1999. Moreover, 0-group sandeel biomass determined by the model in 1999 was higher by a factor of two than in the previous year. Therefore, the first year of the closure was actually preceded by a year of low fishing mortality, combined with reasonable recruit production. Predatory fish biomass in the area was also lower in 1999 than in the two preceding years, presumably resulting in reduced natural mortality, particularly of 0-group sandeels (Greenstreet, 2006). This combination of circumstances allowed 1+ sandeel biomass to increase immediately in the first year of the closure, and to remain at high levels thereafter. The relative contributions of closure of the sandeel fishery, or these other factors, in causing the increase in 1+ sandeel biomass therefore remains debatable. Although not targeted by the fishery, and not appearing in the landings to any significant extent, the model suggested that 0-group sandeel biomass was also higher in three of the four fishery-closure years than in any of the preceding three years, when the fishery was active. These results suggest that the timing of the closure coincided with a period of increased recruit production, and enhanced levels of recruitment to the local sandeel population would certainly have contributed to the increase in 1+ sandeel biomass. At present we are not in a position to speculate as to whether the raised 1+ aged sandeel biomass subsequently contributed to the increase in 0-group sandeel biomass.

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